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THE DIET OF THE SPINY-ANTEATER *TACHYGLOSSUS ACULEATUS ACANTHION* IN TROPICAL HABITATS IN THE NORTHERN TERRITORY

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ABSTRACT

The diet of the Northern Territory "Top-End" echidna, *Tachyglossus aculeatus acanthion*, living in tropical habitats, consists, on average, of about 50% ants and 50% termites as judged by frequency of occurrence in scats. However, at times a majority of ants is eaten, and at other times termites are the predominant food items. Data from a small number of samples gave no indication of change of diet with season. Of 11 genera and 35 species of termites collected in the habitat, 9 genera and 21 species were identified in scats. Of 34 genera and 105 species of ant "identified", 23 genera were found in both scats and collections, but the echidnas consumed six other genera not present in the habitat collections. In one multiple sample 55 species of ant were identified but the overall mean was 14 species per sample. It is concluded that *T. a. acanthion* in a tropical habitat forages opportunistically so that the diet is largely a straight-forward reflection of the composition of the ground-layer ant and termite fauna.

KEYWORDS: Kakadu, echidnas, ants, termites.

INTRODUCTION

The echidna or spiny-anteater, *Tachyglossus aculeatus*, has an Australian-wide distribution including Tasmania and Kangaroo Island. It is found in a variety of habitats ranging from the Simpson Desert to Mt. Kosiusko.

Of the five recognised sub-species of *Tachyglossus aculeatus* (see Griffiths 1978) *T. a. acanthion* is the one found in arid parts of Australia and the Top End of the Northern Territory. This echidna is adapted to the climates of such habitats in that it has very little hair, its pélage being made up largely of stout spines interspersed with a few bristles. Thus it has high conductance (Augee 1978a) enabling it to radiate heat efficiently from its body. However, this is not sufficient to protect it from heat apoplexy if ambient temperatures exceeding 38°C are encountered. The echidna then has to retreat to shady, relatively cool refuges until temperatures fall in the evening allowing it to forage for its prey.

The food of echidnas in southern and central mainland Australia consists almost exclusively of ants and termites, the proportions eaten varying with habitats (Griffiths 1968, 1978, 1989; Abensperg-Traun 1988). Very occasionally moth larvae and small beetles may be eaten. Smith *et al.* (1989), however, have found that the New England Tableland echidna ingests scarab beetle larvae which at times account for 37% of the biomass intake, the rest being ants and termites.

Echidnas capture their ants and termites by the protusion of a long sticky vermiform tongue, to which prey adheres. The tongue also serves to grind the prey into fragments by the reciprocal action of a toothed pad located on the dorsal surface of the posterior end of the tongue. Only the soft parts are digested and the fragmented chitinous exoskeletons of the prey pass out in the faeces, which also contain dirt and sand ingested with the insects. The scats so formed set hard, in a characteristic cylindrical shape, and resist weathering. Most of the chitinous fragments in the scats can be identified under the microscope down to family level and some to genus and species so that estimates of proportions ingested can be made

(Griffiths 1968, 1978; Abensperg-Traun 1988).

The diet of echidnas living in tropical Australia is unknown and since a preliminary survey showed that scats could be collected in sufficient numbers in Kakadu National Park it was decided to carry out a study of the diet of tropical *Tachyglossus aculeatus acanthion* in that region.

STUDY SITES

Kakadu National Park comprises a region upwards of 20,000 square kilometres through which passes a major portion of the South Alligator River (Fig. 1) and to a lesser extent the East Alligator River. Land forms (Christian and Aldrick 1977) consist of woodlands, tributary creeks of the rivers and associated flood plains, a portion of the Arnhem Land escarpment, large outliers of the escarpment and small isolated rain-forest patches.

The dominant feature of the climate is the occurrence of two very different seasons the "wet" and the "dry" (Christian and Aldrick 1977). The wet lasts from November to April. About 80% of the annual rain falls during this period (annual mean recorded at Oenpelli, 1343mm), January to March being the wettest months. The period May to October is one of drought. High ambient temperatures are another feature of the climate and these are sustained throughout the year; the range between mean monthly temperatures is only 5.6°C. October and November are the hottest months exhibiting a mean maximum of about 38°C. The coldest month is July exhibiting a mean minimum of 17°C. Echidnas can cope quite well with cold weather (Augee 1978b) so the mild minimum temperatures of Kakadu's winter would impose no restrictions on foraging activity during that season.

METHODS

Scats were collected over the period 20 February 1980 to 15 October 1981 from four widely separated areas in the Park (Fig. 1): **(1)** Monsoon rainforest at the edge of the East Alligator River flood plain (Fig. 1, location A) and at Radon Creek (location G). **(2)** Cannon Hill, Hawk Dreaming, Obiri Rock and outliers at East Alligator Ranger Headquarters (locations B, C, D and E respectively). **(3)** Djawamba Massif and associated rock outliers, (location F - F). This collection area was some 20 kilometres long and 23 samples were taken at 10 different places. Kerle and Burgmann (1984) have described this part of the study area in detail; it consists principally of dry escarpment and woodland. **(4)** Jim Jim Falls, H. and U.D.P. Falls, I. The distance from location A to I is 130 kilometres. Area 2 has been described as woodland and dry escarpment by Braithwaite *et al.* (1985) and area 4 as wet escarpment and rainforest. The species of termite ocurring in those habitats and monsoon rainforest have also been given by those authors (Table 1). A collection of termites made by us at Djawamba Massif differed in no way from their escarpment collection.

Some background information is available on the ant fauna of Kakadu. In January 1983 ants were sampled with pitfall traps and using cracked-wheat and sardine baits, the latter placed on the trunks of trees and on the ground in a selection of habitats including monsoon forest, open forest, and woodland plots (described by Braithwaite and Dudzinsky 1983); these results are summarized by Greenslade

Table 1. Termites collected at the eastern portions of Kakadu National Park in monsoon rainforest and escarpment. Data from Braithwaite *et al.* (1985, 1988). + Present, - Absent.

	Rainforest	Escarpment
MASTOTERMITIDAE		
Mastotermes darwiniensis Froggatt	+	–
RHINOTERMITIDAE		
Coptotermes acinaciformis Froggatt	+	+
Heterotermes vagus (Hill)	+	–
Heterotermes validus Hill	+	–
Heterotermes venustus (Hill)	+	–
Schedorhinotermes actuosus (Hill)	+	+
Schedorhinotermes breinli (Hill)	+	+
TERMITIDAE		
Amitermes laurensis (Mjöberg)	–	+
Amitermes perelegans (Hill)	–	+
Amitermes sp. A	–	+
Amitermes sp. B	–	+
Australitermes perlevis (Hill)	–	+
Drepanotermes septentrionalis Hill	–	+
Microcerotermes boreus Hill	+	+
Microcerotermes nanus (Hill)	+	–
Microcerotermes nervosus Hill	+	+
Microcerotermes serratus (Froggatt)	+	+
Microcerotermes sp.	–	+
Nasutitermes eucalypti (Mjöberg)	+	+
Nasutitermes graveolus (Hill)	+	+
Nasutitermes longipennis (Hill)	–	+
Nasutitermes sp. A	–	+
Nasutitermes sp. B	–	+
Nasutitermes sp. C	–	+
Occultitermes occultus (Hill)	+	+
Termes froggatti (Hill)	+	+
Termes melvillensis (Hill)	+	+
Termes quadratus (Hill)	+	+
Termes xunteri (Hill)	+	+
Termes taylori (Hill)	–	+
Termes sp. A	+	+
Termes sp. B	–	+
Termes sp. C	+	+
Termes sp. D	–	+
Termes sp. F	–	+

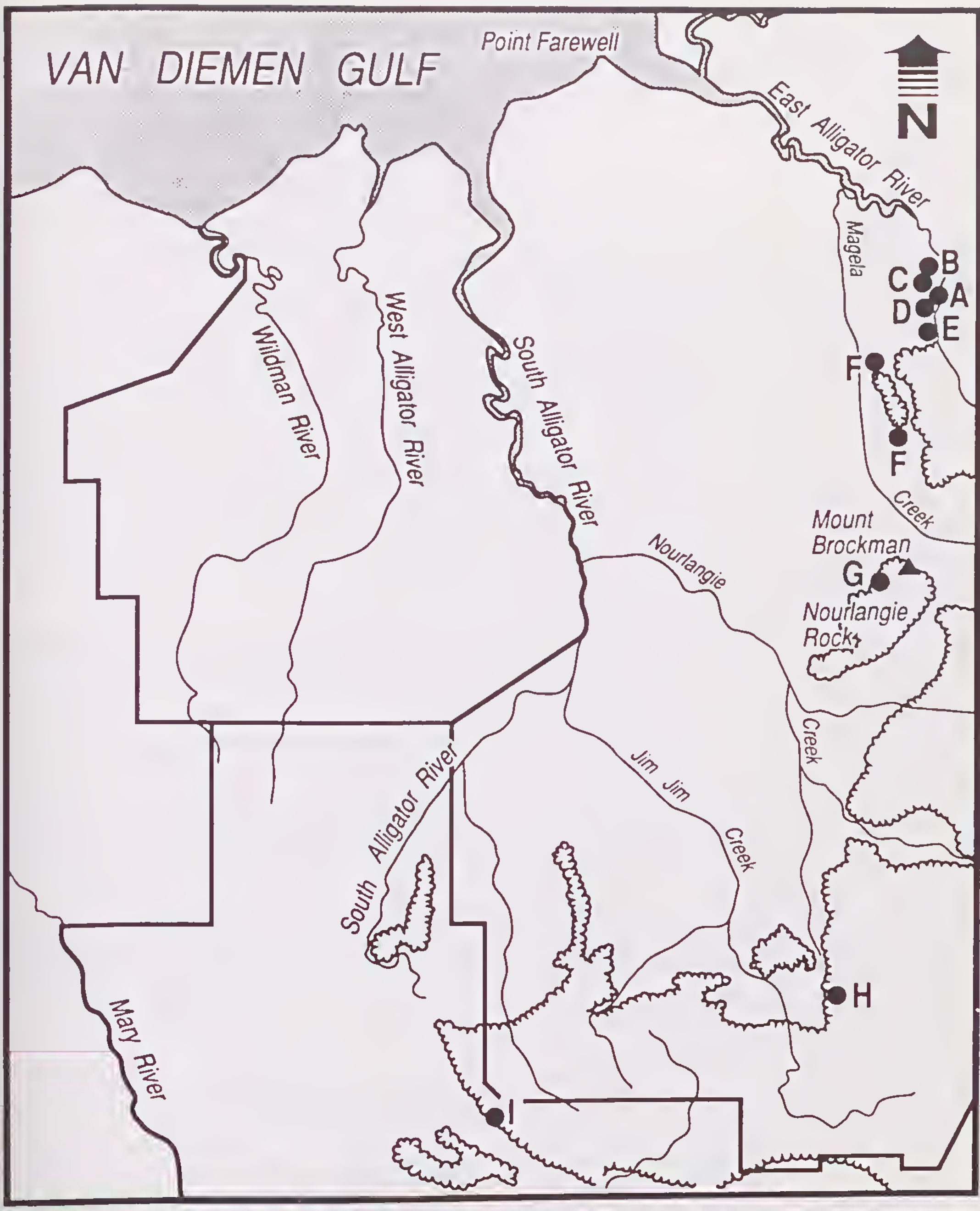

Fig. 1. Map of the Alligator Rivers Region showing the nine localities where echidna scats were collected.

(1985). In May 1983 this sampling routine was repeated. Additional material also came from limited hand collections and Tullgren-funnel extraction of soil and litter (Greenslade, unpublished results). Only a fraction of the ants that were collected can be given specific names but in the January collection 105 species were 'identified', if only by code numbers within genera. A plot of cumulative species against cumulative samples rises steeply to a possible asymptote indicating a tally of 200 species for the region (Greenslade 1985). More recent studies suggest that this is a very conservative figure (A.N. Anderson, personal communication). A list of the genera found is given in Table 7.

Table 2. Frequency of termites and ants in echidna scats collected at the four areas (see text) in the Park.

Collection Area	Number of samples analysed in duplicate	% Termites	% Ants
1. Rain Forest	12	59	41
2. Dry Escarpment	18	56	44
3. Dry Escarpment	23	49	51
4. Wet Escarpment	3	75	25

The scats were found in a variety of places: in the monsoon forest, in exposed areas of escarpment and rock outliers, on sand amongst spinifex clumps on those outliers and in caves and overhangs of the outliers. Some of these scats were quite fresh, being soft, dark and exhibiting a faecal odour, whereas others were of indeterminate age. Scats were between 1.5-6.0 centimetres long.

Most of the samples were of one or two pieces of scat, however, some were multiple samples containing 7-35 pieces. In all, a total of some 170 scats were collected. For dietary analyses these were freed of dirt and sand by trituration with a glass rod in water in a litre Erlenmeyer flask. The flask was then vigorously shaken and immediately filled with water. The chitinous parts floated to the top of the neck of the flask and were removed with a spoon and transferred to 80% alcohol. This procedure was repeated until no more chitin could be obtained. Duplicate aliquots of well-stirred suspensions of the samples in alcohol were transferred to 75 x 100 mm microscope slides, the chitinous parts being spread thinly and evenly as possible. They were then allowed to dry, covered with Canada Balsam and baked in an oven at 50°C. The frequency of ants and termites in the samples was determined by counting the chitinous parts along carefully defined transects of the slides. The parts counted were the head capsules of ants, rostra of nasutitermitine soldiers, jaws of other termite soldiers and jaws of termite workers, the counts of the jaws being divided by two. The choice of these entities for determination of numbers was determined by the observation that the head capsules of the ants and nasute soldiers almost always remained intact whereas the soft head capsules of the other termite castes were crushed by the echidna's grinding pad leading to separation of the jaws which are relatively indestructible. For determination of the ratio of ants to termites ingested, the number of identifications made varied from 88 to 430 per slide depending on the size of the sample available, i.e. about 180-800 identifications per sample. The counts of the duplicates expressed as percentages agreed very well, the average difference being only 4.9% ± 4.7%.

Table 3. Frequency of termites and ants in fresh scats collected at various times of the year at the four areas in the park.

Collection Area	Time of Year	% Termites	% Ants
1	16 September	68	32
	16 September	54	46
	6 November	58	42
2	28 February	40	60
	19 August	65	35
	19 September	74	26
	19 September	73	27
	29 November	47	53
3	28 July	28	72
	24 August	77	23
	26 August	75	25
	4 September	17	83
	22 September	57	43
	26 September	34	66
4	30 March	83	17
	15 October	75	25
	13 November	67	33

The different kinds of termites in aliquots of the samples were identifiable only to subfamily level as judged by the morphology of nasutes, worker and soldier jaws on a quantitative basis (i.e. frequency). Where possible genus and species were identified but no quantitative estimates could be made. Determinations of frequencies of termites were also made in duplicate, a hundred identifications being made each time.

A procedure different from the one described above was adopted for the ant moiety of the diet in view of the very large number of different species that were ingested and which could be 'identified' to species level.

Ants were recorded from aliquots of 30 of the samples, mainly from the single scat samples of Area 3, and from some composite multi-scat samples. Each sample was examined under low magnification in approximately 10ml lots. Two procedures were carried out: firstly in each scat and composite sample all ants were identified to genus and sorted to species within genera from whatever fragments were present, from single mandibles to entire bodies. This provides frequency data: the sum of species per genus per scat or composite sample. Secondly a quarter of each 10ml sub-sample was examined in a gridded dish identifying and counting individual head capsules to genus and, where possible to species giving minimum relative abundance

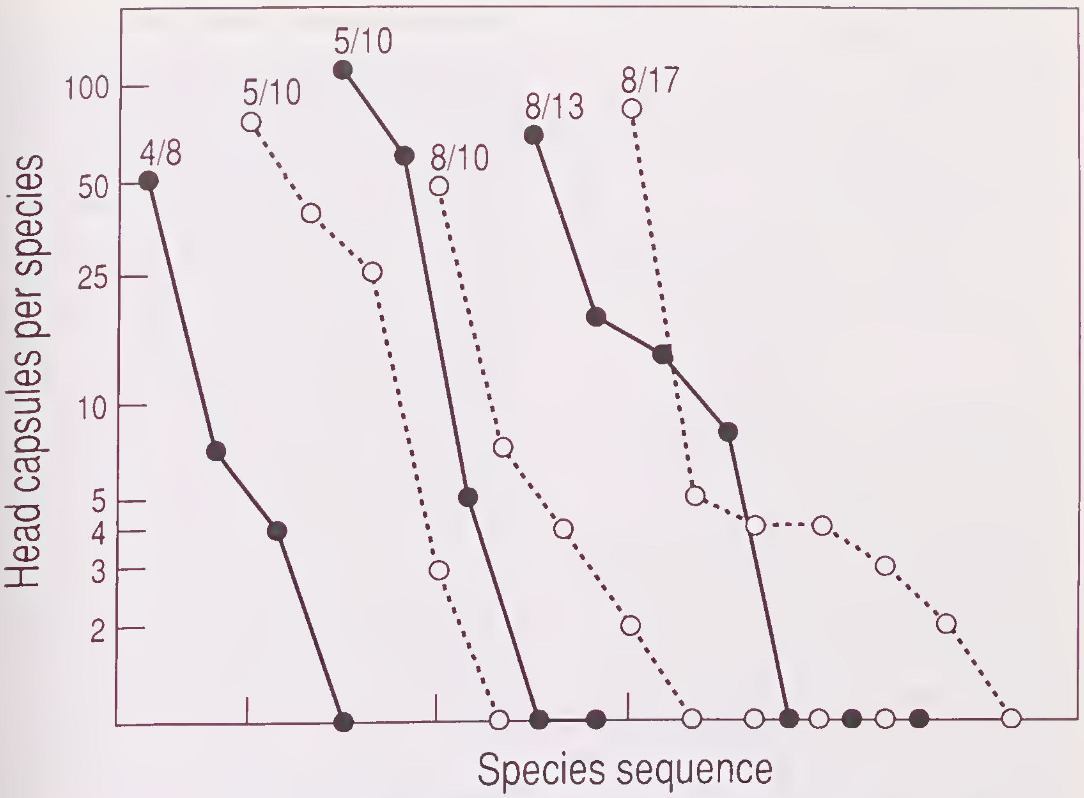

Fig. 2. Statistical distributions of the relative abundances (from head capsule counts) of individual ant species in six echidna scats. Fractions represent: total species in head capsule counts/total species recognized in the sample.

data. This involved 550 species records and counts of 3684 head capsules, averaging 18 species and 120 head capsules per scat or composite sample.

Significance of differences between means was determined by Peritz's F test for multiple comparisons using the computer program written by Harper (1984).

RESULTS

Kinds of food items ingested. Along with a total count of 15,000 ants only 15 individual arthropods, including 8 scarab larvae, were encountered in the samples. All other items were termites. Consequently the Kakadu echidna is overwhelmingly an ant and termite eater.

Ratio of termites to ants ingested. The proportions of ants and termites occurring in the scats from the four areas are shown in Table 2. From this it is apparent that in all areas except Jim Jim - U.D.P. Falls the Kakadu echidna eats roughly equal proportions of ants and termites. The apparent preference for termites in Area 4 is very likely due to the small sample size (n = 3). This is borne out by the wide variation in the type of intake in areas where the sample size was adequate. For example, in Area 3 on eight occasions the frequency of ants exceeded 70% and on the same number of occasions the frequency of termites exceeded 70%. Equally large variations were also found in Area 2 scats. The point is further emphasized in Table 3 in which the results from examination of the fresh scats are given. From these data one can say it is just as likely that the echidnas will be eating more ants than termites or vice versa. Furthermore, there is no evidence from analysis of this small number of fresh samples that there are any seasonal changes in diet.

Termites. Large differences in the kinds of termites ingested are apparent. From the data in Tables 4 and 5 it can be seen that in all the study areas many more Termitidae than Rhinotermitidae were eaten. In areas 1, 2 and 3, where the numbers of samples permitted statistical analysis, the differences between the mean frequencies of Termitidae and Rhinotermitidae were significant ($P<0.0001$).

Table 4. Frequency of termite families identified in scats from monsoon rainforest and wet escarpment habitats.

a. Radon Creek Rainforest

Number of samples	Rhinotermitidae[1]	Termitidae[2]	Mastotermitidae
10	24.1%	75.9%	Nil

[Termitidae comprising: *Amitermes*-group (5.8%), *Termes*- group (45.1%), and Nasutitermitinae[3] (25.0%)]

[1]Rhinotermitidae species identified:	*Coptotermes acinaciformis* *Schedorhinotermes actuosus* *S. breinli*
[2]Termitidae species identified:	*Microcertermes serratus* *M. nervosus* *M. nanus* *M. boreus* *Termes orbus* *T. melvillensis* *T. sunteri*
[3]Nasutitermitinae:	No remains identified beyond subfamily level.

b. Edge of East Alligator River Flood Plain Rainforest

Number of samples	Rhinotermitidae[1]	Termitidae[2]	Mastotermitidae
2	3.0%	97.0%	Nil

[Termitidae comprising: *Amitermes*-group (18.6%), *Termes*-group (26.0%), Nasutitermitinae[3] (51.5%)]

[1]Rhinotermitidae species identified:	*Heterotermes* sp. *Coptotermes* sp.
[2]Termitidae species identified:	*Microcerotermes nervosus*
[3]Nasutitermitinae:	No remains identified beyond subfamily level.

c. Jim Jim and U.D.P. Falls Wet Escarpment

Number of samples	Rhinotermitidae[1]	Termitidae[2]	Mastotermitidae
3	20.1%	79.9%	Nil

Termitidae comprising: *Amitermes*-group (11.0%), *Termes*-group (20.2%), Nasutitermitinae[3] (48.7%)

[1]Rhinotermitidae species identified:	*Coptotermes acinaciformis* *Schedorhinotermes actuosus* *S. breinli*
[2]Termitidae species identified:	*Amitermes* sp. *Microcerotermes* sp. *Drepanotermes* sp.
[3]Nasutitermitinae:	No remains identified beyond subfamily level.

Since species composition of Termitidae in rainforest differed from that of escarpment (Table 1) it was to be expected that differences within that group would be found in scats from the different areas: in Area 1 (Radon Creek) significantly more *Termes*-group termites and Nasutitermitinae were eaten than *Amitermes*-group ($P < 0.0001$ in both instances). It is noteworthy, however, that the echidnas' diet here contained a small percentage of *Amitermes*-group termites whereas Braithwaite *et al.* failed to collect them. The difference between consumption of *Termes*-group termites and Nasutitermitinae was barely significant ($P = 0.016$).

On the other hand in Areas 2 (Cannon Hill etc.) and 3 (Djawawba Massif) many more Nasutitermitinae than either *Amitermes*- and *Termes*-group termites were eaten; these differences between the mean frequencies of the *Amitermes*-group and the *Termes*-group in Areas 2 and 3 were not significant.

Ants. The scats proved to be remarkable for the very wide range of ants that they contained, 55 different species being recognisable in one composite sample. The number of species in individual scats, however, varied from 2-36 (Table 6) with an overall mean of 14.0 species. Given the relative number of scats from different areas or habitats there is no significant departure, as shown by the standard deviations in Table 6, from this overall mean.

Figure 2 shows the distribution of abundances of individual species in a small number

Table 5. Frequency of termite families identified in scats from dry escarpment habitats.

a. Cannon Hill, Hawk Dreaming, Ohiri Rock, East Alligator River Ranger's Head Quarters.

Number of samples	Rhinotermitidae[1]	Termitidae[2]	Mastotermitidae[3]
18	9.1%	90.4%	0.5%

[Termitidae comprising: *Amitermes*-group (21.5%), *Termes*-group (16.8%), Nasutitermitinae[4] (52.1%)]

[1]Rhinotermitidae species identified:	*Coptotermes acinaciformis* *Coptotermes* sp. *Schedorhinotermes actuosus* *S. breinli* *Heterotermes validus*
[2]Termitidae species identified:	*Amitermes* sp. *Drepanotermes* sp. *Microcerotermes boreus* *M. nervosus* *M. serratus* *Microcerotermes* sp. *Termes quadratus* *Termes* sp.

[3]*M. darwiniensis* in 3 scats only

[4]Nasutitermitinae: No remains identified beyond subfamily level, except *Tumulitermes* sp.

b. Djawamba Massif

Number of samples	Rhinotermitidae[1]	Termitidae[2]	Mastotermitidae[3]
23	15.2%	84.6%	0.2%

[Termitidae comprising: *Amitermes*-group (22.2%), *Termes*-group (17.7%), Nasutitermitinae[4] (44.7%)]

[1]Rhinotermitidae species identified:	*Coptotermes acinaciformis* *Schedorhinotermes actuosus* *S. breinli* *Heterotermes* sp. *Heterotermes venustus*
[2]Termitidae species identified:	*Amitermes* sp. *Drepanotermes* sp. *Microcerotermes serratus* *M. boreus* *M. nanus* *M. nervosus* *Termes melvillensis*

[3]*M. darwiniensis* is 2 scats only

[4]Nasutitermitinae: No remains identified beyond subfamily level, except *Tumulitermes pastinator*.

of scats in which all species could be distinguished unequivocally from their head capsules. The general pattern consists of a curve in which a large proportion, 50-80%, of the total number of individuals are contributed by one or a few ant species, with a variable tail of infrequent species. Some nest aggregrations are certainly included in the diet judging by this abundance distribution and the occasional presence of dealate queens and alate sexuals.

Table 7 describes the faunal composition of ants recognised in scats in comparison with what little we know of the regional ant fauna of the Alligator Rivers - Kakadu area.

Despite the fact that most echidna scats came from dry escarpment and woodland, while most information on the ant fauna comes from collections made in open forest and woodland, Table 7, shows a close correspondence at generic level between the two sets of data: of the 34 genera in Table 7, 23 were represented in both. However, five of the genera collected in 1983 were not found in the scats and six were found only in scats. Also the frequencies of three important genera *Iridomyrmex*, *Oecophylla* and *Crematogaster* were lower in scats than would be predicted from the 1983 data. Reasons for these apparent anomalies are discussed below. With these exceptions in taxonomic composition, therefore, the ant component of the diet as shown by the data in this Table seems to be a fair sample of the regional ant fauna, apart from the absence of exclusively arboreal ants. This is supported by the relationship between the frequency of genera in the 1983 collections and their frequency in scats, shown in Figure 3.

However, arboreal species that do forage on the ground as well as on vegetation, notably

Table 6. Summary of echidna scats sorted for ants.

	Area of Collection				
	Monsoon Rainforest 1	Dry Escarpment 2	3	Wet Escarpment 4	Totals
Total Samples	6	6	15	3	30
Total Scats	3	5	15	3	26
Total Species records	164	110	234	42	550
Total abundance	1,004	586	1,762	368	3,720
Mean no. (and range) of species	9.0	12.2	15.6	14.3	14.0
per scat	(7-12)	(2-18)	(5-36)	(9-21)	(2-36)
± S.D.	2.16	5.71	8.55	4.99	7.54

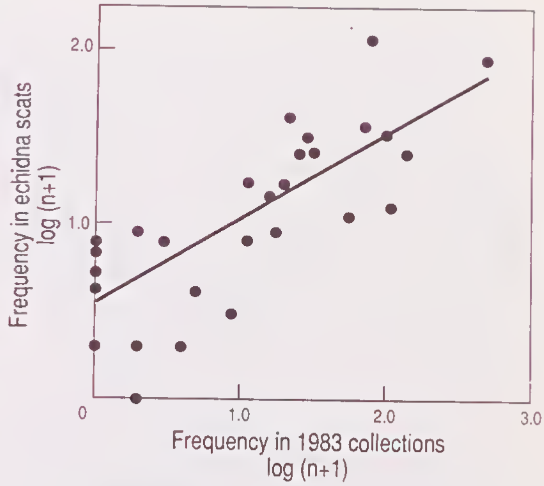

Fig. 3. Relationship between frequency of ant genera in 1983 collection samples and frequency in echidna scats (data double logarithmically transformed); ($r = 0.8$, $P<0.001$, $y = 0.53 + 0.49x$).

Oecophylla smaragdina, are taken and must be captured as individual workers on the soil surface. In fact these arboreal species were more prominent in scats than strictly cryptic species: per cent frequency/per cent relative abundance for cryptic species was 5/2, and for the arboreal species it was 11/4. There is also a close relationship between frequency in scats and frequency in the 1983 collections (Fig. 3 and see Table 7).

When relative abundance in scats was plotted against frequency of occurrence (Fig. 4a) a disproportionately high abundance of *Pheidole* and *Paratrechina* and low abundance of *Rhytidoponera* became apparent. Considering all genera, there is a significant frequency - abundance relationship (Fig. 4a), although with a wide scatter of points for the numerically least important and infrequently represented genera. *Pheidole*, *Paratrechina* and *Rhytidoponera* ranked 1, 3, and 5 in frequency, respectively. If these are excluded there is a very close frequency-abundance correlation for the remaining genera (Fig. 4b) which emphasizes the outlying position of *Pheidole*, *Paratrechina* and *Rhytidoponera* (see Discussion).

Habitat-area distributions of some major ant taxa are shown in Figure 5, although it should be noted that only a small number of scats were examined from some areas (area 4 in particular, Table 6). These data suggest that there is no wide variation at the generic level in the ants taken by the echidnas, regardless of

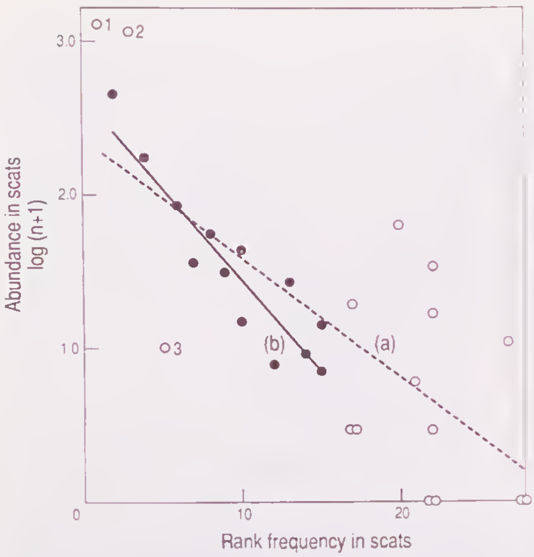

Fig. 4. Relationship between rank frequency of genera in scats and relatively abundance (head capsule counts, log (n+1)). (a) open circles, broken regression line : all genera ($r = 0.76$, $P<0.001$, $y = 2.46 - 0.08x$); (b) solid circles, solid regression line : more frequent genera (up to rank 15) excluding points 1, *Pheidole*, 2, *Paratrechina*, and 3, *Rhytidoponera* (see text) ($r = -0.92$, $P<0.001$, $y = 2.68-0.12x$).

which area scats were obtained, with the exceptions of the leading "dominants" *Oecophylla smaragdina* and *Iridomyrmex sanguineus* (Greenslade 1985). Both of these occurred infrequently and at low abundance. An explanation of this is offerred below.

Table 7. Ants recorded from the Alligator River region from monsoon rainforest, open forest and woodland in January 1983 (Greenslade 1985), with later additions May 1983, and in echidna scats from Area 1, 2, 3 and 4. A, genera containing arboreal nesting species. C, cryptic genera consisting of species entirely or almost entirely restricted to soil and litter. The genus *Chelaner* is provisionally retained despite synonomisation with *Monomorium* (Bolton 1987).

Taxon	January 1983 (species/ frequency)	January+May 1983 (Total species)	Echidna Scats (Frequency/ relative abundance)
PONERINAE			
Anochetus	–	–	7/2
Bothroponera	1/1	3	3/–
Brachyponera C	–	–	1/–
Cerapachys	2/2	3	7/19
Discothyrea C	–	1	–/–
Hyponera C	–	2	3/–
Leptogenys	1/1	2	8/6
Odontomachus	2/54	2	10/8
Rhytidoponera	7/99	10	32/0
DORYLINAE			
Aenictus	–	–	7/61
PSEUDOMYRMICINAE			
Tetraponera A	–	1	–/–
MYRMICINAE			
Cardiocondyla	1/1	2	–/–
'Chelaner'	3/10	9	7/2
Crematogaster A	4/136	5	26/88
Glamyromyrmex C	–	1	–/–
Meranoplus	8/17	15	8/13
Monomorium	15/72	17	34/177
Oligomyrmex C	1/8	1	2/25
Podomyrma	–	1	–/–
Pheidole	12/76	17	110/1462
Quadristruma C	1/1	1	1/–
Solenopsis C	1/10	2	16/43
Strumigenys C	–	–	4/5
Tetramorium	6/15	7	13/9
DOLICHODERINAE			
Iridomyrmex	9/368	11	88/469
Tapinoma	1/4	1	3/34
FORMICINAE			
Camponotus	10/32	13	25/36
Melophorus	8/24	14	24/55
Oecophylla A	1/110	1	12/26
Opisthopsis	3/19	3	17/14
Paratrechina	4/20	7	38/1203
?Plagiolepis	–	–	3/16
Polyrhachis A	3/28	5	21/31
Stigmacros		–	–
3/2			
TOTALS	104/118	156	550/3720

DISCUSSION

In agreement with the findings of Griffiths (1968, 1978, 1989) and Abensperg-Traun (1988) on the diet of echidnas living in arid and southern parts of Australia, the Kakadu echidna is an ant and termite eater. In this respect it is unlike the echidna *T. a. aculeatus* living in the New England tablelands, a significant proportion of whose diet is scarab larvae (Smith *et al.* 1989). This is not surprising since the habitats of the two kinds of echidna are quite different: that of the New England echidna consists of large areas of improved arable pasture infested with scarabs.

The results on the determination of the ratios of ants to termites eaten indicate that the Kakadu echidna is an opportunistic feeder ingesting ants and termites as it encounters them. Whereas some scats show that these echidnas ate a preponderance of ants, others show the opposite, but most scat analyses show that it eats equal numbers of ants and termites. Furthermore, although the data are limited, the results from examination of fresh scats show nothing to indicate that there is any seasonal change in diet.

Of the 11 genera and 34 species of termite known to occur in the region (listed in Table 1), all genera except *Occultitermes* and *Australitermes*, and 21 of these species were identified in the echidna scats. The absence of *Occultitermes* from the diet can be attributed to the fact that it is a minute termite which nests in soil. Similarly, *Australitermes perlevis* is quite rare in both wet and dry seasons (Braithwaite *et al.* 1988). These data again suggest that the Kakadu echidna forages opportunistically, ingesting termites as it encounters them.

In contrast, the results of a detailed analysis of the termite moiety in the scats revealed a different picture, whereby far more Termitidae than Rhinotermitidae were ingested. It might be argued that this is due to the relative scarcity of rhinotermitid termites, but from data listed in Table 8 it is apparent that the abundance of rhinotermitid species found in the escarpment is greater than that of the Nasutitermitinae, which were favoured by the echidnas living in that habitat. A likely explanation for this is that rhinotermitid species were shunned by echidnas, as opposed to the alternative explanation that Termitidae were preferred, since the former have very well-developed chemical defence mechanisms producing a variety of particularly noxious alkanes and ketones (Deligne *et al.* 1981; Moore 1968). Nasutitermitinae also produce defensive secretions but, in anthropocentric terms, the odours of those of *Schedorhinotermes actuosus* and *S. breinli* are revolting, whereas those of Nasutitermitinae are quite pleasant. Although these noxious chemicals are used for the defence of colonies, foraging workers and so on against ants and other invertebrate predators, Deligne *et al.* (1981) remark that "It is conceivable that some of the termite defensive compounds have been evolved as specific vertebrate deterrants. Such a development would ensure that these secretions would be highly adaptive because of their simultaneous deterrency to both predatory invertebrates and termito-phagous vertebrates". Since echidnas have well-developed organs of taste and olfaction (Griffiths 1968), and in view of all the above, we conclude that the Kakadu echidna actively shuns Rhinotermitidae because of the unpalatable nature of their defensive chemicals. In support of this notion is the fact that *T. a. acanthion* in an entirely different

Table 8. Relative abundance of Rhinotermitidae and Nastitermitinae at various places on the Kakadu escarpment during the dry and wet seasons. Data from Braithwaite *et al.*, (1985)

Species	Average Abundnce Index	
	Wet	Dry
Rhinotermitidae (*Schedorhinotermes actuosus, Schedorhinotermes Breinli, Coptotermes acinaciforms*)	1.33	0.58
Nasutitermitinae (*N. eucalypti, N. graveolus, N. longipennis, N* spp A, B, C)	0.46	0.30

part of the continent (the wheatbelt of Western Australia) also shuns Rhinotermitidae in spite of a prevailing abundance of *Coptotermes acinaciformis* (Abensperg-Traun 1988).

The high diversity of species of ants found in the samples (mean of 14 per scat and a maximum of 55 from a composite sample) again suggests that the Kakadu echidna feeds opportunistically. In further support of this notion is that there is no evidence from our data on the distribution and abundance curves of individual species in the scats (Fig. 2) of any directed search by echidnas for, or concentration on, particularly rewarding nests, colonies or foraging workers.

It has already been noted that the ant component of the diet represents a fair sample of the regional ant fauna, with the exception of five genera which are absent: *Discothyrea* (Ponerinae), *Tetraponera* (Pseudomyrmicinae), *Cardiocondyla* (2 spp), *Glamyromyrmex* and *Podomyrma* (Myrmecinae). *Tetraponera* and *Podomyrma* have arboreal nests and rarely forage on the ground and so are not generally available to echidnas. Similarly, one of the *Cardiocondyla* species, forages at high temperatures, at a time when echidnas have retired to refuges. It was recorded only once in the January 1983 collection and has a localized distribution in the area (A.N. Andersen, personal communication). The remaining three species (*Discothyrea*, and *Glamyromyrmex* and the second *Cardiocondyla*) all appear to be uncommmon inhabitants of forest litter.

The six genera found only in scats but not in the general habitat collections were *Anochetus* and *Brachyponera* (Ponerinae), *Aenictus* (Dorylinae), *Strumigenys* (Myrmicinae), *Plagiolepis* and *Stigmacros* (Formicinae). Of these *Brachyponera* cf. *lutea* (identified from a single damaged head capsule) occurs in the Alligator Rivers region (A.N. Andersen, personal communication) but probably only occurs on sandy soils that were not studied in 1983; *Plagiolepis* was very tentatively identified from head capsules - the genus has not been recorded from the area and the specimens closely resembled the head capsules of, and indeed may be, *Crematogaster* species; *Strumigenys* inhabits forest litter which has yet to be intensively sampled; *Aenictus*, *Anochetus* and *Stigmacros* species, although not rare, are only found sporadically and locally (A.N. Andersen, personal communication).

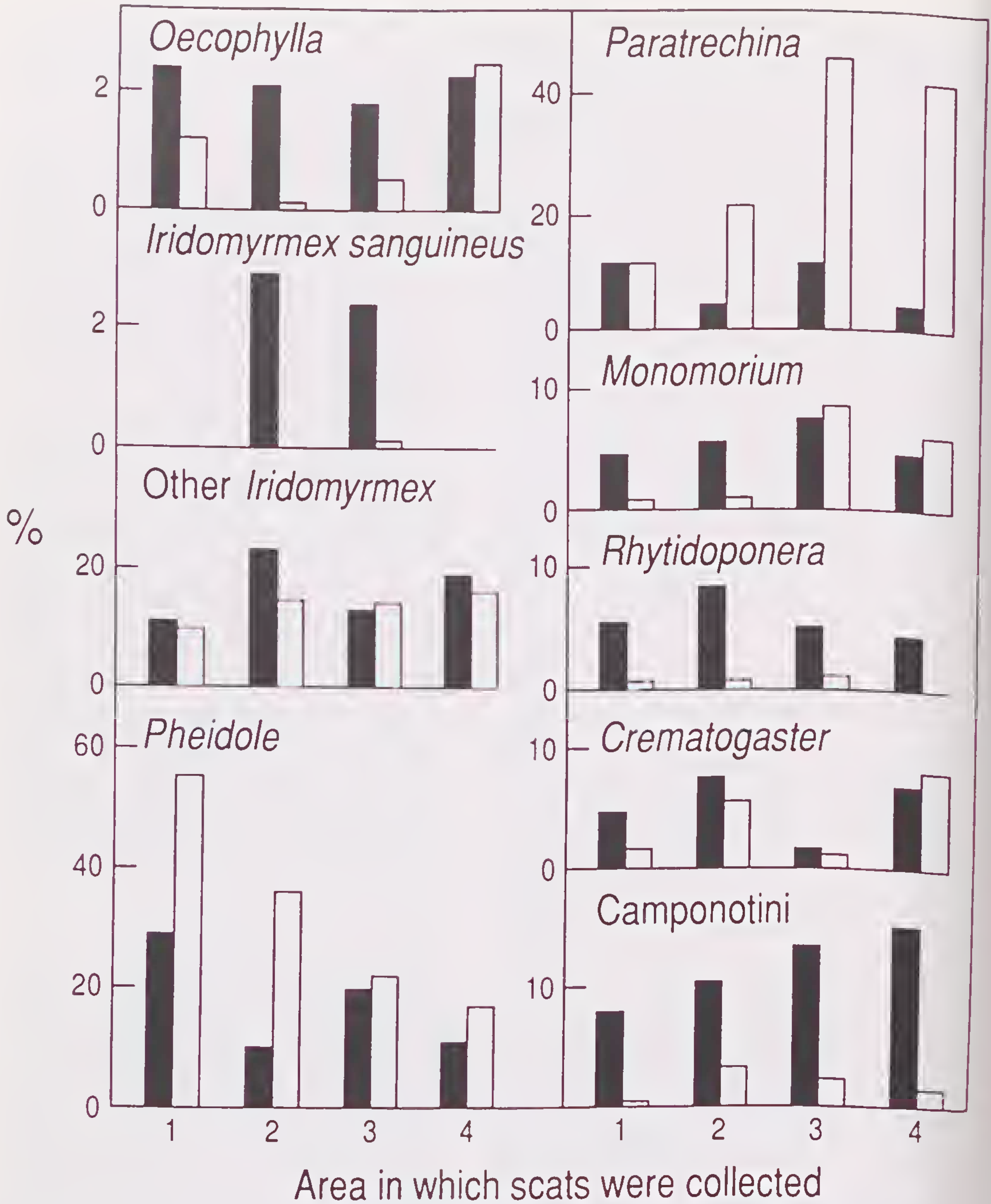

Fig. 5. Distribution (% frequency, solid bars, and % relative abundance, open bars) of some major ant taxa in scats according to area and habitat. Area 1 is monsoon forest, Areas 2 and 3 are dry escarpment, Area 4 is wet escarpment. Note variation of scale of the abscissa. The Camponotini comprised the genera *Camponotus*, *Opisthopsis* and *Polyrhachis*.

The low abundance of *Rhytidoponera* in relation to the apparently high abundances of *Pheidole* and *Paratrechina* in scats (Fig. 4) is accounted for by the fact that the *Rhytidoponera* workers are solitary rather than group- or column-foragers, the echidnas apparently picking up single workers on the soil surface. *Pheidole* and *Paratrechina* are both common genera especially in habitats where the diversity of the rest of the ant fauna is reduced.

They occur in disturbed areas (both genera), on water-logged sites (*Paratrechina*) and on the floor of monsoon rainforest, from which many ants seem to be excluded by shade and low maximum temperatures. An alternative explanation for the high relative abundances of *Pheidole* and *Paratrechina* demonstrated in Figure 4 is that these are a consequence of a relatively low abundance in the echidna's diet of the genus *Iridomyrmex*, even though this is the second-most frequent genus in scats. This does not quite seem to fit the pattern of opportunistic foraging. This applies equally to two other important genera: *Oecophylla* and *Crematogaster*.

The frequencies of these three genera in scats (Table 7, Fig. 5) were lower than would be predicted from the 1983 data, which may be an artefact of the sampling method. Members of these genera are, or include, dominant and strongly territorial species that are frequent at, and monopolize, sardine baits, especially those on trees. Thus, as a measure of importance in the ground layer their frequencies were over estimated by the sampling methods in January 1983. Another contributing factor is that *Oecophylla* and some species of *Crematogaster* are arboreal nesting ants. Consequently, most of these anomalous data are artifacts of sampling.

Despite the fact that *Oecophylla* and the meat-ant, *Iridomyrmex sanguineus* are "dominants" in the Alligator River-Kakadu region, and both exhibit populous colonies and have large-sized workers (Greenslade 1985), both ants were not prevalent and occurred only in low abundance in these scats (Fig. 5). *Iridomyrex sanguineus* was not present at all in scats from Area I, which is monsoon rainforest where the meat ant is not found (Greenslade 1985). In other habitats *I. sanguineus* and *Oecophylla* have mutually exclusive distributions at the colony level: *Oecophylla* was most abundant in the areas in which meat ants were not present in the scats. The infrequency and low abundance of *O. smaragdina* and *I. sanguineus* can be related to the former's primarily arboreal habit, whereas for the latter actual avoidance may be indicated since *I. sanguineus* is a particularly ferocious ant, attacking in large numbers any intruder at the colony. The mound colonies of a closely related and equally ferocious meat-ant, *Iridomyrmex purpureus* (formerly *I. detectus*) are, however, attacked by echidnas during August-October in southern parts of Australia (Griffiths and Simpson 1966), whereas during the rest of the year the colonies are avoided. However, these echidnas at that time are emerging from torpidity or hibernation, and consequently they require energy-rich food. This is supplied by the fat-bodies of the enormous (2 cm body length) virgin queens which come to the surface of the mound at that time of the year. Since this behaviour is a matter of necessity, the echidnas must endure the torment of the bites of the workers to get at the queens (Griffiths and Simpson 1966). This phenomenon would not apply to the Kakadu echidna since ambient temperatures never fall low enough to induce torpor, and consequently the necessity to seek out energy-rich meat-ants does not arise. In all probability the low frequency and abundance of meat-ants in the Kakadu scats can be related to their ferocity.

Another instance of possible avoidance of an ant by echidnas is the fact that the genus *Calomyrmex* occurs at Kakadu, although not abundantly (A.N. Andersen, personal communication), yet it was not recognised in scats. This genus produces a secretion from its mandibular gland which has been shown to be distasteful to, and to repel a number of insectivorous vertebrates (Brough 1978).

CONCLUSION

Abensperg-Traun (1988) found that *T. a. acanthion* living in the wheatbelt of Western Australia forages opportunistically, ingesting its prey - ants and termites - in proportions as encountered. Our study shows that *T. a. acanthion* in tropical habitats likewise forages opportunistically, so that its diet is largely a straightforward reflection of the composition of the ground-layer ant and termite-fauna.

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